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Taxonomic notes on hummingbirds (Aves: Trochilidae). 3. *Heliangelus violicollis* Salvin, 1891 is a color variant of *Heliangelus strophianus* (Gould, 1846)

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Abstract.—The holotype of *Heliangelus violicollis* Salvin, 1891, reportedly from "Sarayacu" on the Amazonian slope of the Ecuadorian Andes, is hypothesized to be a color variant of *Heliangelus strophianus* (Gould, 1846) from the Pacific slope. A second specimen identified by Salvin as an immature male *H. violicollis* represents a female *H. strophianus* in typical definitive plumage. Analysis of plumage color and external measurements revealed no credible evidence for a hybrid origin of *H. violicollis*.

Osbert Salvin (1891:376) characterized *Heliangelus violicollis*, a new sunangel procured by Clarence Buckley in Ecuador, as similar to *H. strophianus* (Gould, 1846), "but the upper surface of a darker, more rufescent brown, especially in the middle of the back; the abdomen too has a more bronzy hue; the most obvious difference is in the colour of the throat, which is glittering violet-blue, without any red or rosy tint." Subsequent taxonomic assessments of *Heliangelus violicollis* were anecdotal. Eugene Simon (cited by Hartert 1897) hypothesized that *H. claudia* Hartert, 1895 and *H. violicollis* represented melanistic color aberrations of *H. amethysticollis* (d'Orbigny & LaFresnaye, 1838) and *H. strophianus*, respectively. Oberholser (1902:333) cast further doubt on the taxonomic validity of *H. violicollis*, noting that gorget colors in *H. strophianus* varied from rose to violet and that "too much importance must not be attached to the precise shade of metallic feathers in separating species of hummingbirds." Cory (1918) listed *H. violicollis* without comment in his catalog, whereas Simon (1921) and Hartert (1922) treated *H. violicollis* as a color variety of *H. strophianus*. Chapman (1926) did not examine the type, but suggested that *H. violicollis* may be the eastern Ecuadorian form of *H. strophianus*. Finally, Peters (1945) recommended that *H. violicollis*, until rediscovered, was best regarded as an aberration of *H. strophianus*. Later treatments either paraphrased Peters (Zimmer 1951, Fjeldså and Krabbe 1990) or omitted *H. violicollis* altogether (e.g., Sibley & Monroe 1990). Nevertheless, the taxonomic status of *H. violicollis* is still very much in doubt, especially in light of recent discoveries of new species of *Heliangelus* with small geographic ranges (Fitzpatrick et al. 1979) or from unknown localities (Graves 1993). Here I provide an assessment of the holotype (BMNH 1887.3.22.901) in The Natural History Museum (formerly British Museum of Natural History), Tring.

Methods

The holotype of *Heliangelus violicollis* was supposedly collected in February 1880 at Sarayacu, Province of Pastaza, on the Amazonian slope of the Ecuadorian Andes (Warren 1966). Chapman (1926:728) noted:

> "birds in this large collection were labeled by the dealer Gerard, Buckley's agent, after they reached London. Most of them are credited to Sarayacu, and

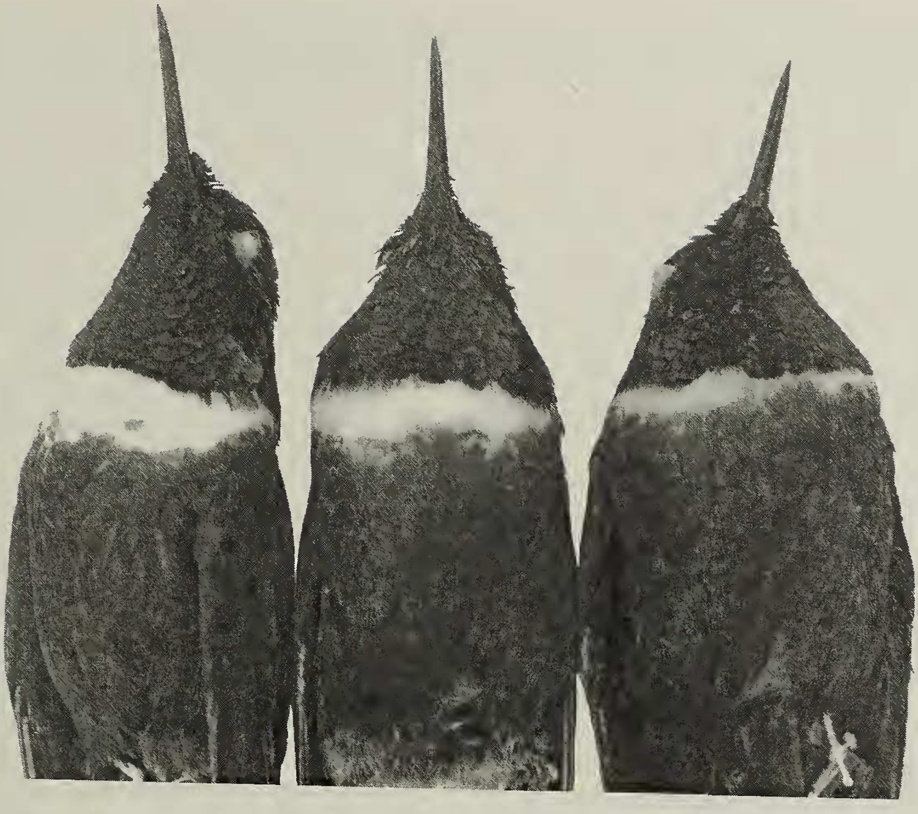

Fig. 1. Ventral view of the holotype of *Heliangelus violicollis* (BMNH 1887.3.22.901) flanked by male *Heliangelus strophianus* in definitive plumage.

this locality on a label attached to a skin from the Buckley collection is therefore to be accepted in a regional sense as any place at or near the settlement of this name and thence to the headwaters of the Rio Pastaza . . . . In this connection it may be added that Buckley employed collectors (Illingworth and Villagomez) in western Ecuador whose specimens were also labeled in London. Not only are the localities attributed to them often misleading, but in some instances it is evident that specimens from Buckley in eastern Ecuador have been confused with those from his collectors in western Ecuador."

Similar misgivings about Buckley's entomological localities were voiced by Brown (1941). Accordingly, the possibility that the holotype of *H. violicollis* was collected on the western slope of the Ecuadorian Andes must be considered.

The unsexed holotype of *Heliangelus violicollis* possesses a large (~53 violet-tipped feathers) gorget and relatively large external measurements (Fig. 1, Table 1), indicative of male plumage in the gorgeted species of *Heliangelus*. A few faint striations (visible at 10X magnification) on the right basal margin of the maxillary ramphotheca indicate the specimen is a young adult (see Ortiz-Crespo 1972). A second specimen (BMNH 2000.1.10) from the Gould Collection reported by Salvin (1891, 1892) as an immature male *H. violicollis* is actually a female example of *H. strophianus* in fairly typical definitive plumage (unstriated maxillary ramphotheca, relatively small external measurements, streaked chin and upper throat small gorget [~10 brilliant feathers], see Bleiweiss 1992). I compared the holotype with all taxa of *Heliangelus* deposited in The Natural History Museum, including the type specimen of *Heliangelus amethysticollis laticlavus* (Salvin 1891) (BMNH 1887.3.22.903).

Table 1.—Measurements (range; mean ± standard deviation in millimeters) of male and female *Heliangelus strophianus* in definitive plumage, the holotype of *Heliangelus violicollis* (BMNH 1887.3.22.901) and a female specimen (BMNH 2000.1.10) of *Heliangelus strophianus* identified by Salvin (1891, 1892) as an immature male of *H. violicollis.*

	Heliangelus violicollis BMNH 1887.3.22.901	*Heliangelus strophianus*		
		Male n = 15–18	Female n = 6	BMNH 2000.1.10
Wing chord	67.6	66.6–70.7 (68.2 ± 1.2)	60.4–62.9 (61.5 ± 0.9)	61.7
Bill length	12.4	12.0–13.5 (12.8 ± 0.4)	12.7–14.2 (13.4 ± 0.5)	12.9
Rectrix 1	38.8	35.2–39.4 (37.1 ± 1.1)	31.9–35.9 (34.3 ± 1.3)	33.8
Rectrix 2	42.3	38.2–42.5 (40.6 ± 1.1)	35.5–39.9 (38.0 ± 1.5)	37.3
Rectrix 3	45.3	41.8–45.2 (43.8 ± 1.0)	36.6–41.7 (39.9 ± 1.8)	39.6
Rectrix 4	47.4	44.0–48.2 (48.8 ± 1.3)	37.1–42.7 (41.0 ± 2.0)	41.5
Rectrix 5	46.5	46.4–50.4 (48.5 ± 1.3)	38.6–42.3 (41.2 ± 1.5)	41.0

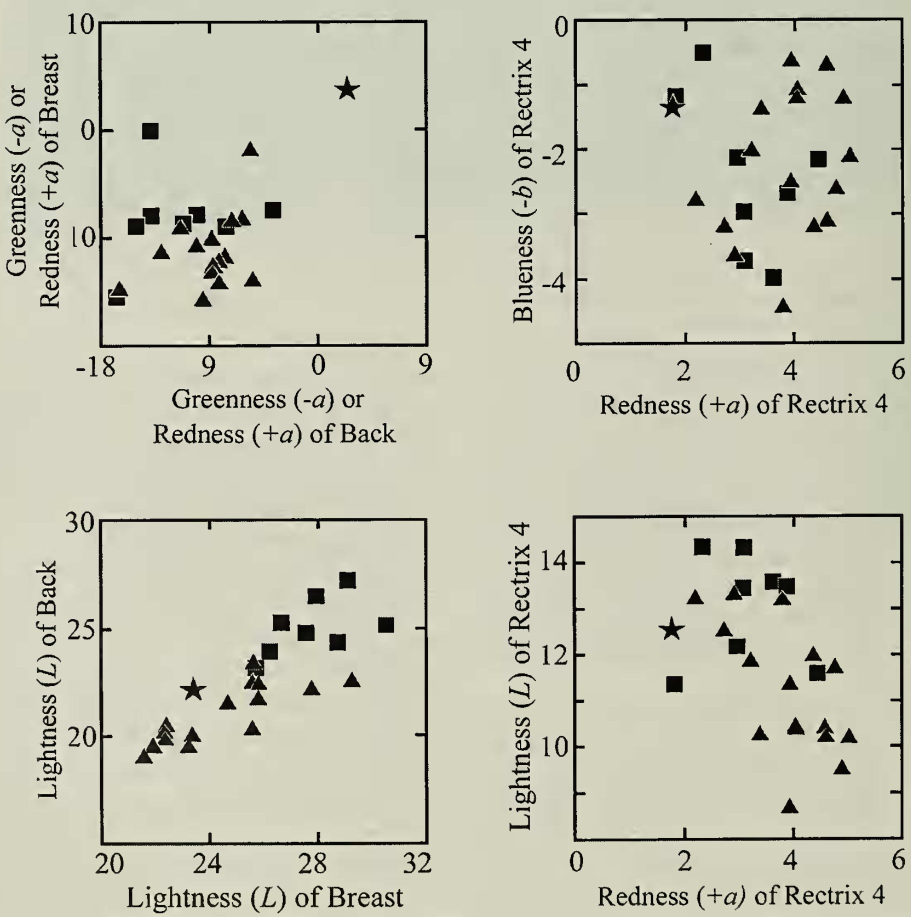

Fig. 2. Bivariate plots of opponent color coordinates (*L*, *a*, *b*) from plumage characters of male (▲) and female (■) *Heliangelus strophianus* in definitive plumage and the holotype of *Heliangelus violicollis* (★) (BMNH 1887.3.22.901).

Table 2.—Minima, maxima, means, and standard deviations of opponent color coordinates (*L, a, b*) reflected from back, crown, breast, and rectrix 4 in male and female *Heliangelus strophianus*, the holotype of *Heliangelus violicollis* (1887.3.22.901) and a female specimen (BMNH 2000.1.10) of *Heliangelus strophianus* identified by Salvin (1891, 1892) as an immature male of *H. violicollis.*

			Heliangelus strophianus						
		Heliangelus violicollis BMNH 1887.3.22.901	Male			Female			BMNH 2000.1.10
			Min.	Max	Mean ± *SD*	Min.	Max	Mean ± *SD*	
Crown	*L*	20.8	18.5	22.1	(20.3 ± 1.2)	22.1	25.4	(23.8 ± 1.2)	21.7
	a	3.6	−9.0	0.3	(−4.9 ± 2.5)	−9.4	0.2	(−4.7 ± 3.6)	−0.8
	b	12.9	13.9	21.6	(17.0 ± 1.9)	15.4	22.1	(18.2 ± 2.8)	15.7
Back	*L*	22.2	19.0	23.4	(20.9 ± 1.4)	23.2	27.3	(25.2 ± 1.3)	24.0
	a	2.4	−16.4	−5.4	(−9.0 ± 2.8)	−16.7	−3.7	(−11.2 ± 4.5)	−13.9
	b	15.9	12.1	22.6	(16.4 ± 2.3)	12.9	23.1	(19.1 ± 3.3)	20.4
Breast	*L*	23.4	21.6	29.3	(24.3 ± 2.3)	25.7	30.5	(28.0 ± 1.6)	26.2
	a	3.8	−15.9	−1.9	(−11.4 ± 3.4)	−15.4	0.0	(−8.2 ± 4.5)	−7.9
	b	13.4	8.6	22.0	(16.4 ± 3.0)	11.0	20.6	(16.4 ± 3.2)	13.4
Rectrix 4	*L*	12.6	8.7	13.3	(11.2 ± 1.4)	11.4	14.3	(13.3 ± 1.1)	11.6
	a	1.8	2.2	5.2	(3.9 ± 0.8)	1.8	3.9	(3.0 ± 0.7)	4.4
	b	−1.3	−4.4	−0.6	(−2.3 ± 1.1)	−4.0	−0.5	(−2.5 ± 1.3)	−2.2

Measurements of wing chord, bill length (from anterior extension of feathers), and rectrix length (from point of insertion of central rectrices to the tip of each rectrix) were made with digital calipers and rounded to the nearest 0.1 mm. Rectrices are numbered from innermost (R1) to outermost (R5).

I evaluated plumage color at five locations with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture: center of crown, at a line drawn across the posterior border of the eye rings; center of back; center of gorget; upper breast, ~4 mm left of the midline below the pectoral band; and the dorsal surface of rectrix 4 near the tip. The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp (C illuminant, 2° observer) is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. In order to reduce measurement variation, I held the aperture flush with the plumage surface without depressing the plumage surface. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure three times for each area of plumage, removing the aperture between trials. Each datum summarized in Table 2 represents the mean of three independent measurements.

Colorimetric data from iridescent gorget feathers are acutely dependent on the angle of measurement, the curvature of the gorget surface in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. Because within-specimen measurement error in *Heliangelus* was deemed excessive, quantitative assessments of gorget color were omitted from data tables.

Colorimetric characters were described in terms of opponent-color coordinates (*L*, *a*, *b*) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (*L*), red-green (*a*), and yellow-blue (*b*). The rationale is that a color cannot be perceived as red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single value *a*, which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by $+b$ for yellows and $-b$ for blues. The third coordinate *L*, ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage the higher the *L* value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans. The relevance of opponent color coordinates to colors perceived by hummingbirds is unknown.

I considered five hypotheses: *Heliangelus violicollis* represents a genetic color variant of *H. strophianus*; an immature plumage of *H. strophianus*; an intrageneric hybrid; a chemically altered or light faded specimen of *H. strophianus*; or a valid taxon. Methods and assumptions of hybrid diagnosis follow Graves (1990) and Graves & Zusi (1990), as modified by insights on plumage color aberrations associated with hybridization (Graves 1998, 1999). Unless noted otherwise, assessments of plumage characters refer to males in definitive plumage.

Results

Plumage and morphological data are consistent with the hypothesis that *Heliangelus violicollis* represents a color variant of *Heliangelus strophianus* (Figs. 1, 2). As indicated by Salvin (1891, 1892), portions of the spinal, capital, and ventral feather tracts that exhibit green iridescence in *H. strophianus* are bronze-colored ($+a$ and $+b$ values in Table 2) in the holotype of *H. violicollis*. Viewed head-on, the crown, lores, auriculars, and sides of the throat are sooty black in both *H. violicollis* and *H. strophianus*. The gorget of *H. violicollis* is slightly smaller and narrower than those of definitive-plumaged males of *H. strophianus*, but this is probably attributable to the slight immaturity of the type of *H. violicollis*. Gorget iridescence is violet in *H. violicollis* as opposed to pinkish-red or rose-red in *H. strophianus*. The size and shape of the pectoral band and pattern of undertail coverts are identical in *H. violicollis* and *H. strophianus*. The rectrices of *H. strophianus* are bluish-black. Those of *H. violicollis* are similar in color, but the central rectrices (R1) are faintly tinted with bronze near the rachis, a trait that is expressed in females and immature males of *H. strophianus*. The external measurements of the holotype of *Heliangelus violicollis* fall within the range of those recorded for male *H. strophianus* in definitive plumage (Table 1). The bronze-colored plumage of *Heliangelus violicollis* differs significantly from that of *H. strophianus* in immature and definitive plumage, indicating that *H. violicollis* is not merely an ontogenic variant of that species.

I found no evidence that *Heliangelus violicollis* represents an intrageneric hybrid. In investigating the possibility of hybridization, I considered five species of sunangels with brilliant gorgets that occur in Ecuador, as potential parental species (i.e., *Heliangelus exortis*, *H. micrastur*, *H. strophianus*, *H. viola*, *H. amethysticollis*; taxonomy of Schuchmann 1999). Only four of the ten possible pairwise combinations of species are known to overlap geographically: *H. micrastur* and *H. amethysticollis*; *H. micrastur* and *H. viola*, *H. exortis* and *H. viola*; *H. amethysticollis* and *H. viola* (Fjeldså & Krabbe 1990, Krabbe et al. 1998). However, based on the prevailing knowledge of plumage inheritance in hummingbird hybrids (Banks & Johnson 1961, Graves 1990, Graves & Zusi 1990, Graves & Newfield 1996), none of the possible species combinations could have produced hybrids with broad white pectoral bands (Fig. 1).

Iridescence in hummingbird plumages can be significantly altered by exposure to light (Graves 1991) or chemicals and may even change over time in sealed museum cabinets in the absence of any direct chemical contamination (Graves 1986). The plumage of *Heliangelus violicollis* exhibits none of the tell tale signs of prolonged exposure to light or chemical alteration of structural color observed in some other 19th century specimens of hummingbirds—e.g., sharp color contrast between exposed and concealed portions of imbricated feathers; asymmetric patterns of iridescence within feather barbs, within feathers, or within plumage tracts; matted or stained feather barbules under magnification; or (4) discoloration of the white pectoral band.

Finally, there is no evidence to suggest that *Heliangelus violicollis* represents a valid taxon. The type locality, Sarayacu (700 m), occurs below the known elevational range of sunangels (*Heliangelus* spp.) in the Andes (Graves 1985, Hilty & Brown 1986, Fjeldså and Krabbe 1990). The failure of 20th century ornithological surveys and collecting expeditions (Paynter 1993) to obtain specimens of *H. violicollis* in the upper Rio Pastaza drainage provides additional evidence, albeit circumstantial, that the holotype was erroneously labeled.

In summary, the holotype of *Heliangelus violicollis* is indistinguishable in size, external shape, and plumage pattern from male *Heliangelus strophianus*, differing only in the color of plumage iridescence. All evidence is consistent with Simon's (1921) hypothesis that *H. violicollis* is a color variant of *H. strophianus*. Consequently, the name *Heliangelus violicollis* Salvin, 1891 is correctly placed in the synonymy of *Heliangelus strophianus* (Gould, 1846).

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